PROC. ENTOMOL. SOC. WASH.
107(1), 2005, pp. 55–63

FOSSIL TRIGONALIDAE AND VESPIDAE (HYMENOPTERA) IN BALTIC AMBER

George Poinar, Jr.

Department of Zoology, Oregon State University, Corvallis, OR 97331-2907, U.S.A. (email: poinarg@casco.net)

Abstract.—A fossil trigonalid (Trigonalidae: Hymenoptera), ***Eotrigonalis balticus*** **Poinar, n. gen., n. sp.,** and a fossil vespid, ***Palaeovespa socialis*** **Poinar, n. sp.,** are described from Eocene Baltic amber. *Eotrigonalis balticus* is a large, robust, heavily armored species, which could have parasitized members of the Vespidae. It can be separated from all other members of the family by the presence of large scutellar horns. *Palaeovespa socialis* has the diagnostic characters of members of the subfamily Vespinae and was probably eusocial. It differs from extant vespines by the shape of the clypeus, the presence of interparapsidal furrows and venational characters.

Key Words: Trigonalidae, *Eotrigonalis baltica,* Vespidae, Vespinae, *Palaeovespa socialis,* Baltic amber

The Trigonalidae are a monophyletic group of enigmatic parasitic wasps comprising some 16 genera worldwide. They have unique morphological characters as well as a complex life history involving both a carrier and a developmental host (Carmean 1991, Carmean and Kimsey 1998, Weinstein and Austin 1991). Fossil trigonalids are rare (Carpenter 1992, Rasnitsyn and Quicke 2002) and the present study describes a new genus and species from Baltic amber.

Social wasps belonging to the subfamily Vespinae of the family Vespidae are not commonly fossilized in amber (Carpenter 1992, Rasnitsyn and Quicke 2002) and the present study describes a new species in Baltic amber closely related to extant members of the genus *Vespula* L. The fossil vespid is a potential developmental host for the Baltic amber trigonalid.

Materials and Methods

The pieces of Baltic amber containing the trigonalid and vespid originated from the Kalinigrad region in Russia. Both pieces were recut and repolished for study. The final piece containing the trigonalid fossil weighed 1.6 grams, was 20 mm long, 13 mm wide and 5 mm deep. The piece containing the vespid fossil weighed 2.6 grams, was 20 mm long, 19 mm wide and 11 mm in depth. Baltic amber has been dated at ~ 40 million years (Eocene) [for a discussion of the age of these deposits, see Poinar (1992) and Larsson (1978)]. Observations and photographs were made with a Nikon Optiphot microscope and a Nikon SMZ-10× stereoscopic microscope at magnifications of ×800. Terminology follows that presented by Huber and Sharkey (1993), Mason (1993), Brothers and Finnamore (1993) and Duncan (1939) with some traditional venation terminology as used by Michener et al. (1994). All measurements are in millimeters unless otherwise noted.

Trigonalidae Cresson, 1887

The Baltic fossil possessed the following characters, which are diagnostic for the family Trigonalidae (Carmean 1991, Carmean and Kimsey 1998, Mason 1993): 23 antennal segments; the presence of groups of white setae on the outside of the middle antennal segments, fore wing with a stigma and 10 closed cells, Cu deflected abruptly posteriorly at the base of 1 m-cu, vein 2 cu-a less than half as long as vein 1 cu-a, veins 2 r-m and 2 m-cu present, veins C and R separate, forming a long narrow costal cell; hind wing with 2 closed cells; claws cleft with arolia; apicoventral plantar lobes present on tarsomeres 1–4, hind trochantellus divided; metasoma pedunculate and ovipositor reduced.

This specimen is nearly complete, with only the apical portions of the right fore and hind wings, a portion of one antenna and the tarsi of the right hind leg missing. Portions of the head are covered with bubbles, which make examination of the mouthparts difficult.

Eotrigonalis Poinar, new genus

Type species: *Eotrigonalis baltica* Poinar.

Description.—Body large, length, 11.3; antenna with 24 segments; lateral posterior borders of scutellum each with a large horn; crossvein 1 cu-a straight, meeting M vein.

Diagnosis.—Only on some extant specimens indicated as belonging to the genus *Xanthogonalos* Schulz (1907) and on the Early Cretaceous *Albiogonalys elongatus* Nel et al. (2003) does crossvein 1 cu-a meet M vein. Other venational differences and the large horns on the scutellum separate *E. balticus* from all known extant and extinct genera.

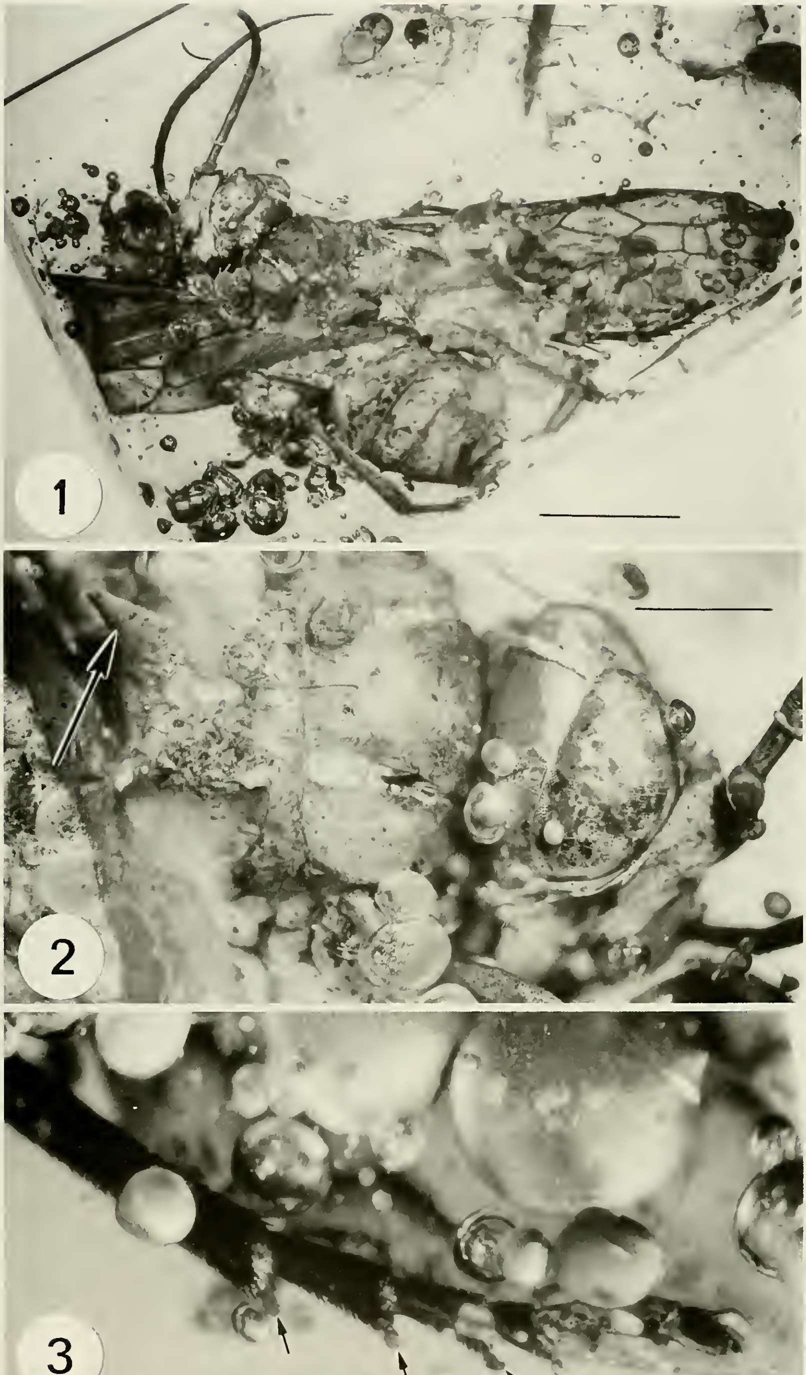
Etymology.—Eo is from the Greek "eos" for dawn, early. This gender is masculine.

Eotrigonalis balticus Poinar, new species
(Figs.1–3, 6–10)

Description.—Holotype female; with characters listed under generic description.

Head: Large, 2.9 long (without mandibles), setae absent except for very short hairs on clypeus; eyes protruding, length eye, 1.8; width eye, 1.2; torulus located beneath a ridge below middle point of compound eye; malar space short; mandibles toothed, asymmetrical, left mandible with 3 teeth, right mandible with 4 teeth; palpal segments obscured by debris; antenna 8.7 long, with 24 segments which taper toward apex; lengths of segments as follows: 1, 0.45; 2, 0.25; 3, 0.60; 4, 0.60; 5, 0.70; 6, 0.55; 7, 0.50; 8, 0.45; 9, 0.40; 10, 0.40; 11, 0.35; 12, 0.30; 13, 0.30; 14, 0.25; 15, 0.30; 16, 0.30; 17, 0.30; 18, 0.25; 19, 0.25; 20, 0.25; 21, 0.25; 22, 0.20; 23, 0.15; 24, 0.35; outer areas of antennal segments 9–20 with patches of raised white setae (or scales).

Mesosoma: 3.3 long; pronotum short, not visible from above, length mesoscutum, 1.5; width mesoscutum, 3.1; length scutellum, 1.8; width scutellum, 1.8; length propodeum 0.6, width propodeum, 1.2; two slightly oblique vertical rows of foveae occur on mesoscutum, latero-posterial corners of mesoscutum projecting outward; a single transverse row of foveae along anterior margin and a medial vertical row of foveae on scutellum; latero-posterior corners of scutellum bearing large robust horns; mesopleuron large, with medial vertical row of foveae; fore and hind coxae contiguous, mid coxae slightly separated; hind leg with divided trochantellus; leg measurements: fore leg, coxa, 0.88; trochanter, 0.74; femur, 0.17; tibia, 1.4; middle leg, coxa, 0.97; trochanter, 0.56; femur, 2.64; tibia, 2.3; hind leg, coxa, 1.32; trochanter, 0.65; femur (with trochantellus); 3.34; tibia, 3.14; tarsal segment lengths: foreleg, T1, 0.97; T2, 0.44; T3, 0.23; T4, 0.21; T5, 0.44; middle leg, T1, 1.17; T2, 0.21; T3, 0.35; T4, 0.26; T5, 0.35; hind leg, T1, 1.65; T2, 0.50; T3, 0.38; T4, 0.29; T5, 0.44; tarsomeres 1–4 on all legs with apicoventral plantar lobes; paired claws cleft, large arolia; wings hyaline, membrane bare; length forewing, 11.0; length hind wing, 7.6; venation as in Figs.7–8; in hind wing, Rs not reaching wing margin, distal part of M not reaching



Figs. 1–3. *Eotrigonalis balticus* in Baltic amber. 1, Lateral-dorsal view. Note attenuated antennal segments. Scale bar = 3.1 mm. 2, Head and mesosoma. Note horn (arrow) on scutellum. Scale bar = 1.0 mm. 3, Apico-ventral plantar lobes (arrows) on first 4 tarsal segments of right leg 3. Scale bar = 0.5 mm.

wing margin, distal part of Cu reaching wing margin, cu-a short, oblique, 10 hamuli present, positioned in distal half of wing, as shown in Fig. 8.

Metasoma: 5.5 long; greatest width, 4.5; tergites with light and dark zones; dark zones confined to bands along posterior borders of tergites 2–7; small ovipositor anterior of cerci.

Material examined.—Holotype female in Baltic amber, deposited in the Poinar collection (accession # Hy-10–180) maintained at Oregon State University.

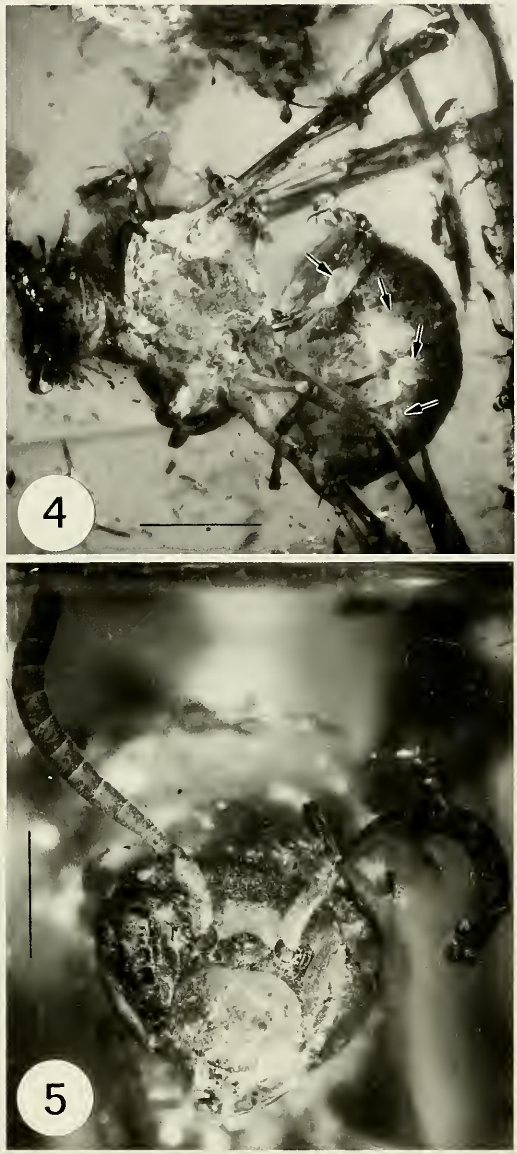
Etymology.—The name is derived from Baltic amber.

Discussion.—This is the first described Tertiary trigonalid. Several Cretaceous trigonalids have been described, but according to Nel et al. (2003), all of these have uncertain family affinities except *Albiogonalys elongatus* Nel et al. (2003), and possibly *Cretogonalys taimyricus* Rasnitsyn (1977). Wing venation, mesosomal armature, number of antennal segments and size separate *E. balticus* from all previously described extinct and extant trigonalids.

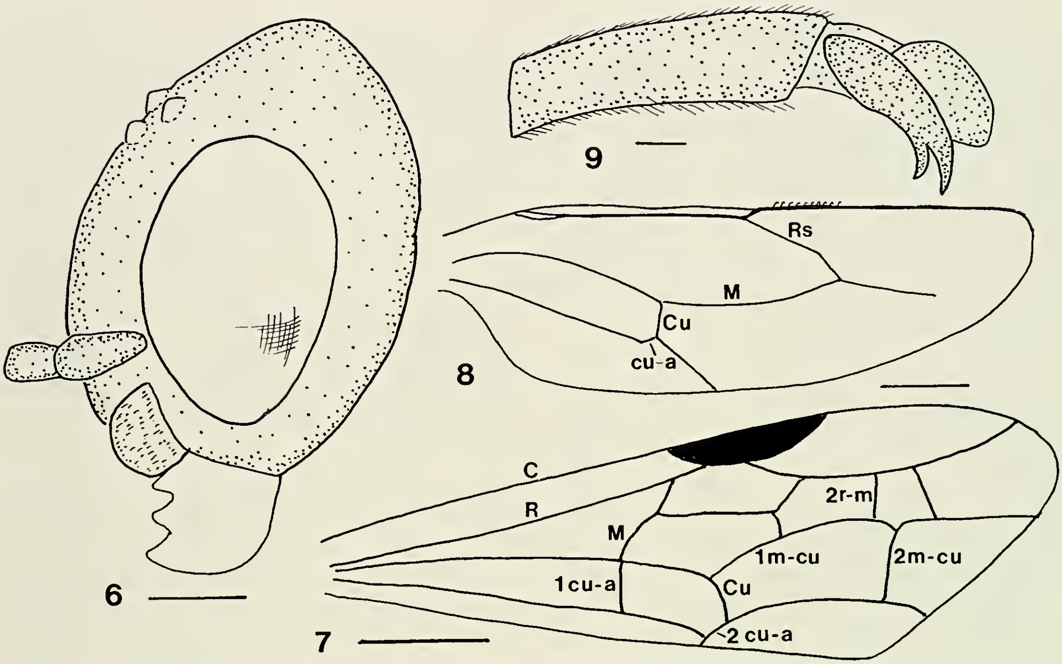
The large size, thick cuticle and armature of *E. balticus* suggest that it was parasitic on an aggressive insect, possibly a member of the Vespidae. Its size, mesosomal armature and wing venation is similar to that of extant members of *Bareogonalos canadensis* (Harrington 1896), a Pacific Northwest species that parasitizes yellow jackets (Carmean 1991). Possible hosts for *E. balticus* might have been members of the genus *Palaeovespa,* one of which is described below. There is only one extant species of trigonalid in Europe, *Pseudogonalos hahnii* (Spinola), which has been reared from Lepidoptera pupae that have been parasitized by Ichneumonidae and Diprionidae (Carmean and Kimsey 1998). Wing venation and scutellar horns separate *E. balticus* from *P. hahnii.*

Vespidae Leach, 1815

This specimen is complete and clearly visible. The hind wings are located under the fore wings and it is difficult to delineate their veins, however no jugal lobe could be detected. This character, along with the sessile metasoma, abruptly declivous tergum 1, absence of parategula, simple, smooth tarsal claws, fore wing with first subdiscal cell



Figs 4–5. *Paleovespa socialis* in Baltic amber. 4, Lateral view. Note yellow bands (arrows) on distal edges of metasomal tergites. Scale bar = 2.5 mm. 5, Face view showing yellow areas between toruli and on scapes and clypeus. Scale bar = 1.2 mm.



Figs. 6–9. *Eotrigonalis balticus* in Baltic amber. 6, Head. Scale bar = 0.6 mm. 7, Fore wing. Scale bar = 1.4 mm. 8, Hind wing. Scale bar = 1 mm. 9, Penultimate tarsal segment of left fore tarsus with cleft claws and empodium. Scale bar = 63 μm.

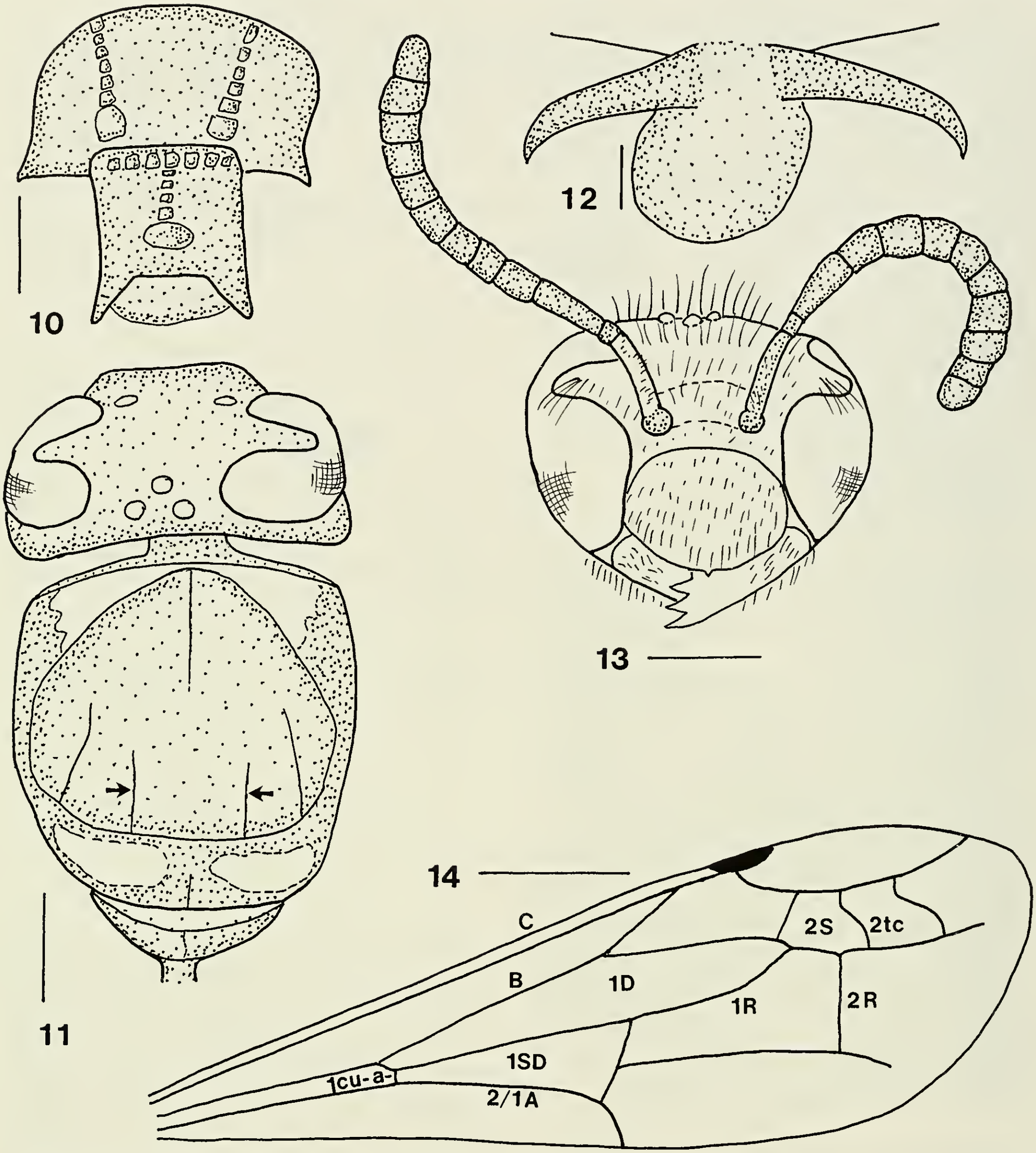
neither narrowed nor projecting apically, metacoxae with a dorsal longitudinal carina, fore wing with vein 1 cu-a (cu-v) straight and much shorter that vein 2/1A and with the apex of the marginal cell not separated from anterior margin of wing, place the specimen in the eusocial subfamily Vespinae (Brothers and Finnamore 1993).

Characters which place the specimen in the genus *Palaeovespa* Cockerell 1906 are the oblique apex of the first discoidal cell, the recurrent veins joining the second submarginal cell near its ends and the basal vein joining the costal vein near the stigma. The genus *Palaeovespa* was erected for several species described from the Florissant deposits (Cockerell 1906). Later Cockerell (1909) described *P. balticus* from Baltic amber, assigning it to this genus on the basis of similar wing characters. Since the present fossil possesses similar venational characters, it is placed in *Palaeovespa*.

Palaeovespa socialis Poinar, new species
(Figs. 4–5, 11–14)

Description.—Holotype female; total length, 12.8. *Head:* Length, 2.6 (without mandibles), head bearing long setae (except eyes), greatest width head, 3.5, clypeus wider (1.6) than high (1.2), light in color, basal margin convex with small medial projection; ocelli positioned close to occiput; antenna 12 jointed, segments thick, third segment nearly as long as scape; compound eyes deeply emarginate; light (yellow) area between toruli; malar space short; mandibles with three sharp teeth and an inner molar area; a light yellow genal band extends a short distance behind each eye; scapes and clypeus yellow.

Mesosoma: 3.8 long, bearing long setae; black except for following light areas: anterior border of mesoscutum, edges of metanotum (a pair of light areas), scutellum



Figs. 10–14. Fossil Trigonalidae and Vespidae in Baltic amber. 10, Mesoscutum and scutellum of *Eotrigonalis balticus.* Scale bar = 1 mm. 11, Dorsal view of head and mesosoma of *Palaeovesoa socialis* (setation not shown). Arrows show interparapsidal furrows. Scale bar = 1 mm. 12, Simple tarsal claws of the left mesotarsus of *P. socialis* with basal bristles and empodium. Scale bar = 63 μm. 13, Face view of *P. socialis.* Scale bar = 1 mm. 14, Fore wing of *P. socialis.* B = basal vein, C = costal vein, 1D = discal cell, 1R = first recurrent vein, 1SD = first subdiscal cell, 2R = second recurrent vein, 2S = second submarginal cell, 2tc = second transverse cubital vein. Scale bar = 0.9 mm.

(two light areas) and sides of propodeum; mesepisternum with a pair of light spots on sides; mesoscutum with a mesidan notal suture, two parapsidal furrows and two shorter furrows between parapsidal furrows (termed interparapsidal furrows); length fore wing, 8.5; apex of first discoidal cell oblique; basal vein meets costal vein near stigma, distance from apex of basal vein to stigma, 135 μm, wing membrane covered with minute setae; legs with yellow and black markings; leg measurements: fore leg, coxa, 1.0; trochanter, 0.4; femur, 2.0; tibia, 1.9; tarsus 1, 1.2; (rest of tarsus not visible); middle leg, coxa, 0.5; trochanter, 0.3; femur, 2.2; tibia, 1.8; tarsal segments, T1, 1.0; T2, 0.3; T3, 0.3; T4, 0.3; T5, 0.6; hind leg, coxa, 0.8; trochanter, 0.4; femur, 1.6; tibia, 2.2; tarsal segments, T1, 2.8; T2, 0.4; T3, 0.3; T4, 0.4; T5, 0.4; tarsal claws simple, each with a basal seta; empodium large.

Metasoma: Length, 6.4; tergites with proximal portions black, distal areas yellow; stinger protruding.

Material examined.—Holotype female in Baltic amber, deposited in the Poinar amber collection (accession # H-10-175) maintained at Oregon State University.

Etymology.—The name *socialis* refers to the likely social habit of the specimen.

Diagnosis.—This specimen has many features of extant members of the genus *Vespula,* including the short malar space, ocelli located at edge of vertex, eyes deeply incised, longitudinal carina on the dorsal side of the metacoxa and coloration (Duncan 1939). While the color patterns are mainly light and dark, yellow shades in many of the light areas suggest that the true colors were black and yellow. The diagnostic characters mentioned above, especially the absence of parategula and simple, smooth tarsal claws, place *P. socialis* in the Vespinae.

Earlier reports of Vespidae in Baltic amber include *Vespa dasypodia* Menge (1856), the description of which is limited to roughly a half page, without illustrations. The location of this specimen is unknown. However several characters separate this species from *P. socialis.* In *V. dasypodia,* the ocelli are arranged in almost a straight line, which differs from the triangular position in *P. socialis.* Also *V. dasypodia* has reddish- yellow hairs on the ventral surface of the first tarsal segment of the fore leg and hirsute hairs on the first tarsal segments of the middle and hind legs. Such hairs are lacking in the present specimen. Menge (1856) also stated that the posterior portions of the 4th, 5th and 6th abdominal sternites of *V. dasypodia* are covered with short bristles, which is not the case in *P. socialis.*

The second Baltic amber vespid was a brief description of *Palaeovespa baltica* Cockerell (1909). Cockerell used venational characteristics to align *P. baltica* with the Nearctic *Palaeovespa* species, however, it is questionable whether the former species belongs to the same genus as the New World fossils.

Size differences between *P. baltica* and *P. socialis* do occur (*P. baltica* is 16 mm in length with a wing length of 11 mm in contrast to 12.8 mm and 8.5 mm, respectively, for *P. socialis*) but they could represent caste or individual differences. However coloration differs between the two species. In *P. baltica* the apical portion of the abdominal segments, the venter, legs and wings are ferruginous, which is not the case in *P. socialis.* There are also wing venational differences. In *P. socialis,* the end of the second transverse cubital vein turns abruptly and meets the marginal cell at a right angle. This angle is oblique in *P. baltica.* The distance from the apex of the basal vein to the stigma is 425 μm in *P. baltica,* but only 225 μm in *P. socialis.* A major difference between *P. socialis* and modern vespines is the shape of the clypeus and the presence of interparapsidal furrows on the mesoscutum, but these characters were not included in the description of *P. baltica.*

The species of *Palaeovespa* from the Florissant shales (Cockerell 1906, 1917, 1923) are described mainly on size and color variations, which could indicate caste, colony or individual differences. The Florissant fossils differ from *P. socialis* in both size and coloration. Lengths are 14.5 mm for *P. gillettei* Cockerell, 18 and 22 mm for two specimens of *P. scudderi* Cockerell, 25 mm for *P. florissantia* Cockerell and 17.5

mm for *P. relecta* Cockerell. Regarding coloration, *P. gillettei* has two longitudinal yellow stripes on the mesothorax and a dark area on the apical part of the costal cell, which is lacking in *P. socialis. Palaeovespa scudderi* has apical light areas on only the last 2 abdominal segments (all abdominal segments have apical light areas in *P. socialis*), *P. florissantia* has no distinct abdominal markings but reddish wings and *P. relecta* has the head and thorax black, the first two abdominal segments pallid, with small lateral dark markings, and abdominal segments 3 to 5 with broad dark bands. These color patterns differ from those on *P. socialis.* Unfortunately very few body characters are described in the Florissant specimens, including the shape of the clypeus and presence of interparapsidal furrows on the mesoscutum.

Discussion.—The present fossil is considered eusocial since it possesses the basic characters of present day Vespinae, all members of which are eusocial today (Brothers and Finnamore 1993). The most obvious difference between *P. socialis* and extant Vespinae is the shape of the clypeus and the presence of interparapsidal furrows on the mesoscutum (Duncan, 1939). In addition, M_{3+4} is much more oblique than on extant Vespines and the second recurrent vein is perpendicular to the second submarginal cell in *P. socialis* but oblique in extant vespines (Duncan 1939). The mandibles of *P. socialis* are clenching a morsel of tissue with crochets, thus indicating that caterpillars were used as a protein source for the larvae.

Acknowledgment

I thank Roberta Poinar for comments on an earlier draft of this manuscript.

Literature Cited

Brothers, D. J. and A. T. Finnamore. 1993. Chapter 8. Superfamily Vespoidea, pp. 161–278. *In* Goulet, H. and J. T. Huber, eds. Hymenoptera of the World: An Identification Guide to Families. Publication 1894/E, Research Branch, Agriculture Canada, Ottawa, 668 pp.

Carmean, D. 1991. Biology of the Trigonalyidae (Hymenoptera), with notes on the vespine parasitoid *Bareogonalos canadensis.* New Zealand Journal of Zoology. 18: 209–214.

Carmean, D and L. Kimsey. 1998. Phylogenetic revision of the parasitoid wasp family Trigonalidae (Hymenoptera). Systematic Entomology 23: 35–76.

Carpenter, F. M. 1992. Superclass Hexapoda, pp.468–495. *In* Kaesler, R. L., ed. Treatise on Invertebrate Paleontology, Arthropoda 4, Part R, Vol. 4, The Geological Society of America, Inc., Boulder.

Cockerell, T. D. A. 1906. Fossil Hymenoptera from Florissant, Colorado. Bulletin of the Museum of Comparative Zoology 50: 33–58.

———. 1909. Descriptions of Hymenoptera from Baltic amber. Mitteilungen aus dem Geologisch-Palaeontologischen Institut und der Bernsteinsammlung der Universität Königsberg 50: 1–20.

———. 1917. Descriptions of fossil insects. Proceedings of the Biological Society of Washington 30: 79–81.

———. 1923. Two fossil Hymenoptera from Florissant (Vespidae, Megachilidae). Entomological News 24: 270–271.

Duncan, C. D. 1939. A contribution to the biology of North American vespine wasps. Stanford University Publications in the Biological Sciences 8: 1–272.

Huber, J. T. and M. J. Sharkey. 1993. Chapter 3. Structure, pp. 13–59. *In* Goulet, H. and J. T. Huber, eds. Hymenoptera of the World: An Identification Guide to Families. Publication 1894/E, Research Branch, Agriculture Canada, Ottawa, 668 pp.

Larsson, S. G. 1978. Baltic Amber—A Palaeobiological Study. Entomonograph, Vol. 1. Klampenborg, Denmark, 192 pp.

Mason, W. R. M. 1993. Chapter 11. Superfamilies Evanioidea, Stephanioidea, Magalyroidea, and Trigonalyoidea, pp. 510–520. *In* Goulet, H. and J. T. Huber, eds. Hymenoptera of the World: An Identification Guide to Families. Publication 1894/E, Research Branch, Agriculture Canada, Ottawa, 668 pp.

Menge, A. 1856. Lebenszeichen vorweltlicher, im bernstein eingeschlossener thiere. Programm öffentlichen Prüfung der schüler der Petrischule, Danzig. A. W. Kafemann, 42 pp.

Michener, C. D., R. J. Mcginley, and B. N. Danforth. 1994. The bee genera of North and South America (Hymenoptera: Apoidea). Smithsonian Institution Press, Washington, DC, 209 pp.

Nel, A., V. Perrichot and D. Néraudeau. 2003. The oldest trigonalid wasp in the Late Albian amber of Charente-Maritime (SW France) (Hymenoptera: Trigonalidae). Eclogae geologica Helvetica 96: 503–508.

Poinar, Jr., G. O. 1992. Life in Amber. Stanford University Press, Stanford, California, 350 pp.

Rasnitsyn, A. P. and D. L. J. Quicke, eds. 2002. History of Insects. Kleuver Academic Publishers. Dordrecht, 517 pp.

Schulz, W. A. 1907. Hymenoptera. Fam. Trigonaloidea. *In* Wytsman, P. ed. Genera Insectorum, Fasicle 61. Verteneuil et Desmet, Brussels. 24 pp.

Weinstein, P. and A. D. Austin. 1991. The host relationships of trigonalyid wasps (Hymenoptera:Trigonalyidae), with a review of their biology and catalogue to world species. Journal of Natural History 25: 399–433.